FOSSIL MAMMALS AND EARLY EOCENE NORTH ATLANTIC LAND CONTINUITY

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ABSTRACT

Until recently American vertebrate paleontologists, particularly students of fossil mammals, have not generally accepted the concept of a former continuous land area around the north end of the Atlantic, connecting western Europe with North America. G. G. Simpson developed biological arguments based on fossil mammals supporting the *existence* of a corridor (Simpson, 1953 and references cited there) topologically connecting western Europe with North America in the early Eocene, but Simpson was influenced by the stabilistic geologic rationale of the times when he located the *position* of the corridor in Asia because of supposed permanence of the Atlantic oceanic barrier during all of Tertiary time. He did not take into account the epicontinental Turgai Straits sea barrier in Asia that lay athwart his corridor in the early Tertiary. The plate tectonic geophysical synthesis of the history of the North Atlantic and Arctic Oceans is in accord with the mammalian timing evidence that a former Euramerican landmass as well as a biota was severed about 49 m.y. ago and that Holarctic land dispersal since that time has been via Asia alone, becoming possible again with Europe in the mid-Tertiary. Earlier, starting about 70 m.y. ago, a continental collision whose site is now within northeastern Siberia created land continuity between what were then Asia and North America, and by the Oligocene the Turgai Straits had finally dried, giving the Holarctic corridor essentially its present configuration. Shallow epicontinental waters have on several occasions crossed Beringia, as at present. Thus the land surface of Holarctica has been rearranged substantially since 70 m.y. ago, North America as a land surface having shifted its allegiance from Europe to Asia.

Recently published geological and geophysical information also suggests that, in addition to early Eocene land continuity in the Greenland-Barents Shelf area, a subaerial dispersal route crossing the volcanic Wyville Thompson Ridge from southeastern Greenland to the Faeroes and then to Great Britain and Ireland may also have been possible for a time in the early Tertiary. This latter route is the long familiar but hypothetical Thulean Bridge, now given a new lease on life by geophysical studies of "hot spots."

Aside from the time-honored and romantic concept of Atlantis, a rationale for a former North Atlantic land area connecting western Europe all the way to the North American mainland can be traced back at least to the 1850's. The concept reached a high level of credibility among biogeographers such as Scharff (1907, 1909, 1911) and geologists such as Arldt (1917), and the connection was usually thought of as operating up until rather late in the Cenozoic. It should be recalled that until Nansen's historic voyage in the Fram in 1893–1896 it was generally believed that the Arctic Ocean was shallow and that a significant amount of unknown land still lurked in those waters—land that might somehow have been a terrestrial dispersal route in pre-glacial times. In its extreme form, the idea of a transatlantic late Cenozoic land bridge in the north is still with us (*e.g.*, Strauch, 1970), although the postulated locale is regarded as Iceland rather than farther poleward. On the other hand various authors, for instance Simpson (1953, 1965), Schwarzbach & Pflug (1957), and Schwarzbach (1959), have claimed that no connection between Iceland and the British Isles existed after the Eocene or that none existed at all during the whole Cenozoic Era. Still other authors have sug-

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gested that an Eocene and earlier route was possible in the far north between Greenland and the now mostly submerged Barents Shelf. A few timid souls have hedged their bets by suggesting that both a far northern and an Icelandic route once existed.

Two types of evidence, geological and biological, can be brought to bear on the problem. Before synthesis, these should be kept separate as long as possible in order to avoid circular reasoning. The biological evidence for a biota presumably occupying a former land continuity across the site of the present water barrier connecting the Atlantic with the Arctic Ocean has been discussed with varying results by many authors, either on the basis of low resolution data from distribution of many kinds of present day organisms or on the basis of high resolution data from less numerous and diverse fossils. The low resolution data have naturally given low resolution answers concerning existence, location, and timing, but the high resolution biological data from dated faunas showing high taxonomic resemblance at low taxonomic rank demonstrates that in early Eocene time, about fifty million years ago, a generalized track (Croizat, 1964; Rosen, 1974) for mammals and presumably other terrestrial organisms did exist somewhere between western Europe and North America across the site of the present marine barrier and did not exist to the east of Europe. But exactly where was this track?

Within the last decade both the direct geological evidence for the necessary continuous solid ground substrate for a land continuity and the indirect biological evidence of the biota that must have existed on it before continuity was broken have become less vague. The generalized track has been transformed through new synthesis from a disembodied topology (in the sense of Croizat) to a new geometry. Power of resolution in viewing the subject in all its complexity has increased markedly, so that now rather than dealing with questions of whether and if, we deal in more detail than ever with when, where, and how. Information from vertebrate paleontology, geology, and geophysics has become sufficiently abundant and its analysis sufficiently coherent not only to lend credence to the notion of former continuous land around the north end of the Atlantic Ocean within Cenozoic time, but also to suggest that, although the route was once a major feature of Holarctic paleogeography, continuous land along the entire route cannot have been present after the early Eocene. Although many proponents of North Atlantic land continuity have made the additional conclusion that continuity still existed as late as the end of the Tertiary, the last time that this was the case for the entire route from western Europe across the present northernmost Atlantic to the North American mainland appears instead to have been almost 50 million years ago.

But, until recently, American vertebrate paleontologists, particularly students of fossil mammals, have not generally accepted a North Atlantic land continuity, at least for the duration of the Cenozoic Era. Simpson (e.g., 1953) developed biological arguments on the basis of fossil mammals supporting the *existence somewhere* of a corridor—in other words a land continuity across which high taxonomic resemblance of a relatively balanced biota prevailed from end to end with dispersal occurring in both directions at the same time for various taxa—
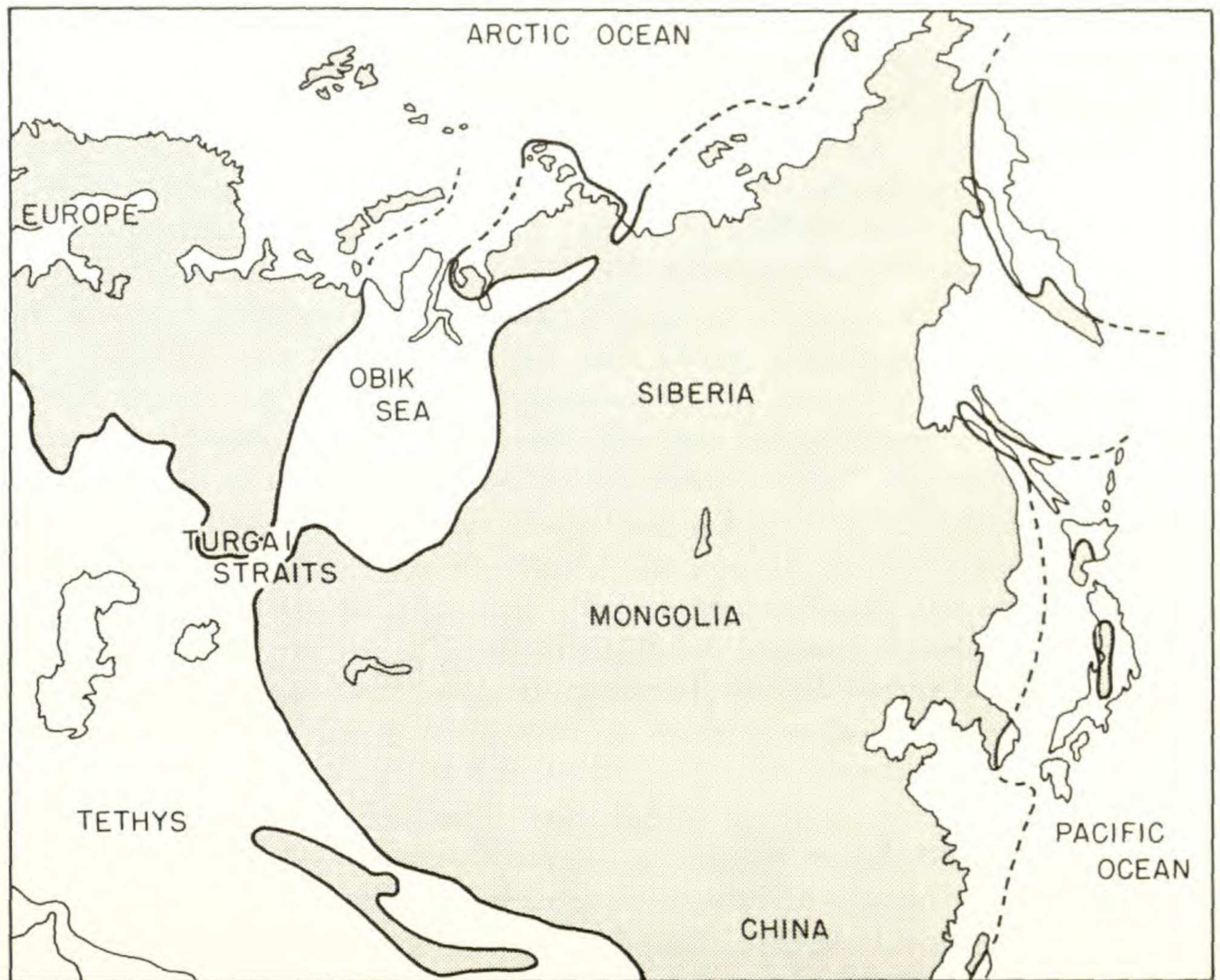
FIGURE 1. Paleogene seaway through the west Siberian lowlands, connecting Tethys to the Arctic Ocean. Based on Zaklinskaya (1970: fig. 47) and differing in detail but not in fundamental features from maps prepared by Sinitsyn (1965) and Dashkevich (1969).

connecting western Europe with North America in the early Eocene (Sparnacian), but he assigned the *position* for the corridor as stretching from western Europe *eastward* to America by way of Asia and Beringia in the same part of the world where continuity indeed existed in the late Cenozoic. The geological rationale prevailing among North American geologists in the 1940's and 1950's was stabilistic, continents and oceans being considered to have had about the same position in the remote past as they have now, so the northernmost Atlantic area was rejected by Simpson and others as a possible early Eocene site for the corridor between North America and western Europe, even though the generalized track for a large number of kinds of early Eocene mammals passed through what is now an oceanic barrier. In addition to the error generated by acceptance of the stabilistic geological model, Simpson did not take into account the epicontinental Turgai Straits marine barrier (Fig. 1), which in the early Tertiary still ran northward from the Tethys Ocean to the Arctic across Asia (Sinitsyn, 1965; Dashkevich, 1969; Zaklinskaya, 1970) and which therefore still prevented continuity of a land biota in that area, thus disrupting Simpson's corridor if its position were postulated to be across that region in the Eocene. Actually, Simpson's biological and statistical evidence for a corridor somewhere at an

undefined position is still basically valid, but his synthesis of biological evidence with incorrect geological information was wrong and simply led to an incorrect location of the early Eocene corridor.

Most importantly, the Eocene break-up of a formerly continuous Euramerican terrestrial biota was masked by Simpson's and other vertebrate paleontologists' acceptance of the stabilist model which, because of its incorporation of a permanent Atlantic-Arctic oceanic barrier, denied that there was an early Eocene Euramerican biota to break up in the first place. In what might be termed the pre-plate tectonic geographic model, the concept of Holarctic continuity via Beringia was extended more or less indefinitely into the past, whereas recent geophysical work suggests that not only the long-lasting (apparently Jurassic through late Eocene) Turgai Straits marine barrier but also a now-vanished oceanic barrier that crossed northeastern Siberia until about 70 million years ago (Pitman & Talwani, 1972; Herron et al., 1974) served to break up Holarctic continuity in the late Mesozoic within what is now Asia. Thus the land surface of Holarctica has been rearranged substantially since 70 million years ago, North America as a land surface having shifted its allegiance from Europe to Asia.

The essence of the plate tectonic reconstruction of the late Cretaceous to present-day geological evolution of the north end of the Atlantic Ocean and its connection with the Arctic Ocean is that about 63 million years ago an extension of the North Atlantic began to open by means of ocean floor spreading between Greenland and Norway in addition to continued spreading in the Labrador Sea. Previous to that time, from about 80 to 63 million years ago, the pole of opening for the North Atlantic had been near northern Greenland (Herron et al., 1974: fig. 5), with compression rather than extension taking place beyond that pole. (Poles of opening have to do with Eulerian rotation of rigid plates on the surface of a sphere, not magnetic poles or the earth's pole of rotation.) Spreading ceased altogether in the Labrador Sea about 45 million years ago as calculated from the magnetic anomaly time-scale (Phillips & Forsyth, 1972) or 48 million years ago as calculated by Hyndman (1973) on the basis of age/depth relations. Meanwhile Greenland and Svalbard slid past one another along transform faults in the Spitsbergen Fracture Zone as Greenland and Norway separated. The nature of the Spitsbergen Fracture Zone offset between the Nansen (Gakkel) Ridge and Atka Ridge sections of the northward extending mid-Atlantic/mid-Arctic ridges has been explained by Wilson (1965), Vogt et al. (1970), and Pitman & Talwani (1972) as a transform fault system (Fig. 2). In terms of the magnetic anomaly time-scale Greenland and the Barents Shelf (including Svalbard) finally parted company at about the same time that ocean floor spreading in the Labrador Sea ceased. This break in formerly continuous continental crust at the northeastern corner of Greenland is in reasonably close agreement with an abrupt fall-off in similarity at the generic and higher levels between the mammalian faunas of western Europe and North America dated as occurring about 49 million years ago by K-Ar techniques applied to volcanic rocks and glauconites associated with the mammalian fossils. This fall-off, discussed but not fully documented in recent years (Kurtén, 1966; Russell, 1968; Savage, 1971; Hartenberger, 1972), has been
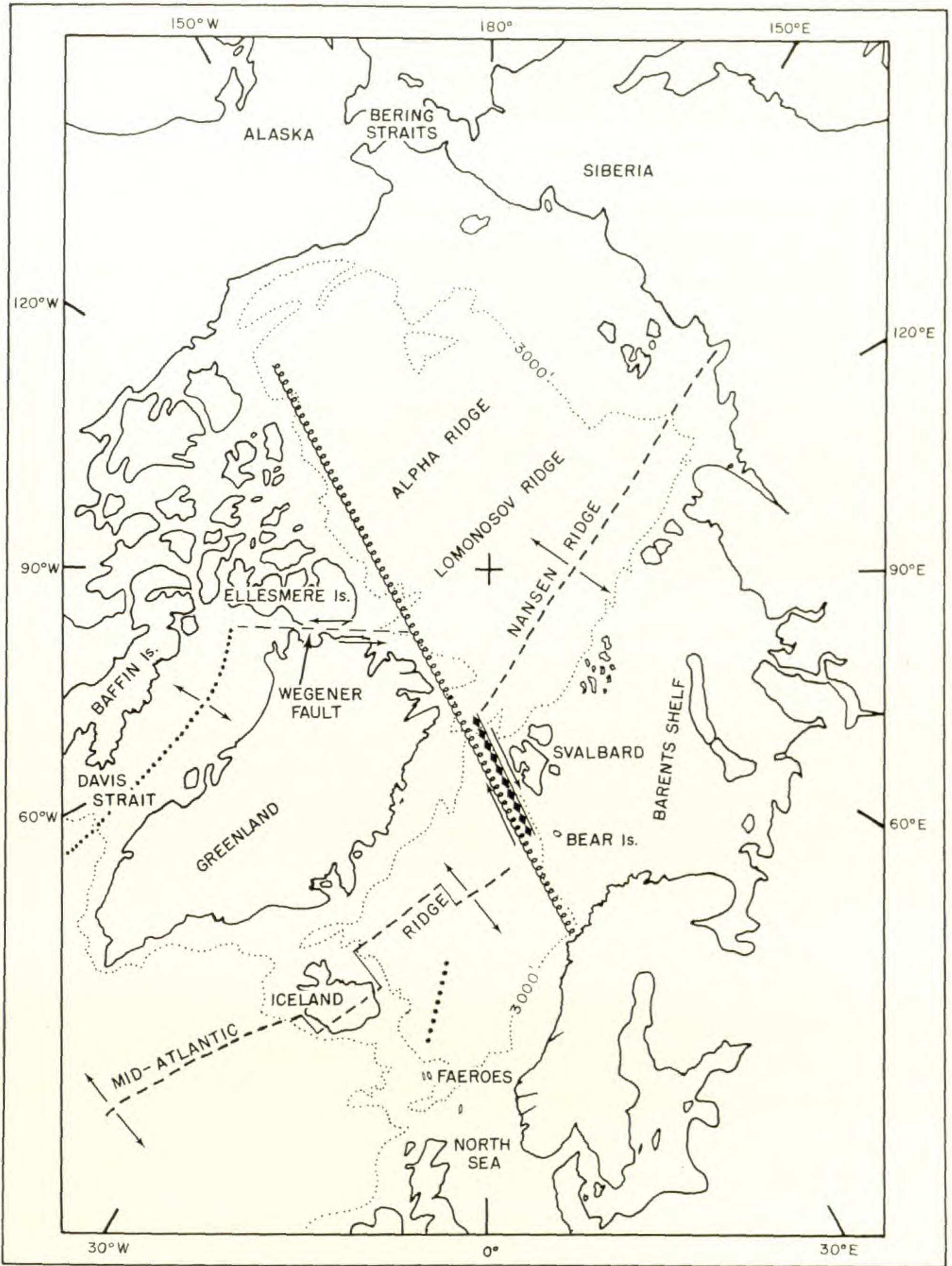
FIGURE 2.   Present-day North Atlantic, Greenland and Norwegian seas, and Arctic Ocean, showing De Geer Line (coil) and major transform fault offset of spreading axis along Spitsbergen Fracture Zone (diamonds). Arrows show motion of newly generated oceanic crust. Modified after Wilson (1965).

explained as the natural consequence of final break-up of the land surface of Greenland from Svalbard and a postulated subaerial Barents Shelf (Szalay & McKenna, 1971; McKenna, 1972a, 1972b) rather than as a result of submergence of some part of a formerly continuously subaerial Brito-Arctic (Thulean Basaltic) Province (Holmes, 1918; Washington, 1922: 780) along a route following the ridge from southeastern Greenland to the Faeroe Islands, then south to Great Britain and Ireland and from there to nearby areas in western Europe.

The driving mechanism for this plate separation has been suggested to be mantle plumes underlying "hot spots" (Wilson, 1963, 1965; Morgan, 1971, 1972; Vogt, 1971; Burke et al., 1973; Schilling, 1973). Recent papers by proponents of plumes revitalize the concept of a formerly subaerial continuity between the northern British Isles and Greenland because they suggest a mechanism for the generation of subaerial aseismic ridges which later sink beneath sea level when ocean spreading has proceeded for a sufficient length of time.

The purpose of this paper is to present and interpret the fossil mammalian evidence concerning an ancient North Atlantic land continuity in somewhat greater detail than I have done previously and to review some recently published information which among other things suggests that, in addition to the eastern part of the De Geer Route (McKenna, 1972a, 1972b) across the Barents Shelf to Greenland, continuity of the now sundered Brito-Arctic Province between present-day southeastern Greenland and Great Britain and Ireland may indeed have provided an alternate, more southerly land connection from western Europe as far west as Greenland during part of the early Tertiary as various authors such as Schulz (1894) and Gregory (1929) have previously suggested for late Cenozoic time on geologically and geophysically insufficient grounds. Between Greenland and Canada, however, it appears that Davis Strait and Baffin Bay already had become an oceanic barrier by the early Tertiary; for this reason any possible land continuity between Greenland and Canada must have been north of Baffin Bay.

PHYSICAL SETTING FOR CONNECTING ROUTES

The De Geer Route (McKenna, 1971, 1972a, 1972b; Szalay & McKenna, 1971) in the far north via Svalbard to Greenland and the more southerly Thulean Route (Strauch, 1970) from the British Isles to Greenland have been discussed by many authors but the basis has usually been biogeographic rather than geological. In the following section of the paper I wish to discuss briefly the rudiments of the physical setting for these proposed routes, reviewing information that is either well known, new, or newly interpreted as exploration of the North Atlantic ocean floor has become more complete.

NORTHERN ROUTE

The De Geer Route is simply a result of constructing the pre-drift position of the Barents Shelf, including Svalbard, with regard to Greenland and Ellesmere Island (see Pitman & Talwani, 1972: fig. 8). Presumably, contact of European continental crust with that of North America was maintained for some time after

the start of continental separation in the area because of the nature of the transform fault system represented by the Spitsbergen Fracture Zone. Most of what is believed to have happened in the area results from studies of ocean floor spreading histories of both near and distant areas applied to theoretically rigid plates moving on the surface of a sphere, thus predicting what must have occurred at a distance, but the history of northern Greenland and the Barents Shelf and its islands is now known well enough to contribute its own share of significant information (Wegmann, 1948; Harland, 1969; Orvin, 1940).

The Barents Shelf lies beneath a shallow epicontinental sea stretching from the mainland of Norway northward to Svalbard and Franz Joseph Land and reaching eastward to the twin islands of Novaya Zemlya. A fall in sea level or an uplift of the sea floor of between 250 and 300 m today would result in continuous land from Svalbard to northern mainland Norway either along a more or less direct route following the 40° E meridian or along an indirect route eastward via a high at about 78° N to the 55° E meridian and then south to Novaya Zemlya and the mainland. Between Bear Island and Norway's North Cape, water more than 400 m and locally 500 m deep occupies what appears to be a large drowned drainage system. Smaller apparent drainage systems exist to the west and also to the southeast of Franz Joseph Land.

Nansen (1904) believed that sea level has risen to its present level only since Plio-Pleistocene times. Because he could find no general cause for simultaneous subsidence of diverse coastlines and shelves on the sides of what are now known to be expanding ocean basins, he opted for general changes in sea level to explain the effect. Nansen's value of 400–500 m higher elevation with respect to sea level than today for the Barents Shelf in late Tertiary time and Orvin's (1940) figure of 500 m are based on the concept that the postulated Barents Shelf drainage systems were once subaerial. Either shelf uplift or a sea level drop of 500 m would put the present surface of a continuous Svalbard-mainland land connection at least 200 m above present sea level, to which must be added whatever amount erosion may have reduced that land surface before it was submerged. Preglacial worldwide oceanic volume was somewhat higher, not lower, than at present because of Quaternary water commitment to polar ice caps, but the amount would not be sufficient to drown the Svalbard-mainland connection. The depressing effects of Quaternary ice loading, if any, on the Barents Shelf are unknown. Presumably the Barents Shelf has on occasion stood somewhat higher than at present and is not always an epicontinental marine barrier to terrestrial dispersal.

The present flora of Svalbard has about 160 indigenous vascular plants, of which 120 also occur in northern mainland Scandinavia (Rönning, 1963). About 35 species have high Arctic distribution and do not occur on the mainland. Among the latter are a number of species shared only with Novaya Zemlya (Rönning, 1963: 103). This is compatible with, but of course does not prove, a former direct subaerial connection between these islands via the Barents Shelf. The time of submergence is unknown but could have been in the late Cenozoic.

Lowell (1972) has recently reviewed the structural evolution of the main island of Svalbard, to which the name Spitsbergen has now been restricted. He

found clear evidence of combined right lateral and compressive motion along and parallel to the Spitsbergen Fracture Zone, which has folded and thrust various Precambrian to Mesozoic rocks along the west coast and folded Tertiary sediments in southern Spitsbergen that some workers have thought to be as young as Miocene in age (Flood *et al.*, 1971). Lowell attributed the termination of folding and thrusting to the northwestward departure, beyond the Spitsbergen Fracture Zone, of the continental crust of Greenland, an event which he dated at 15 million years ago on the basis of assumptions that the spreading half-rate north of Iceland has been 1 cm year^{-1}, that such an average has been maintained, that a distance of 300 km of transform motion since the event has taken place, that the compression had to be caused by the pressure of continental crust from across the fracture zone, and that Spitsbergen's continental Tertiary is correctly dated. These assumptions are debatable and are subject to adjustment. Separation of the blocks containing Greenland and Norway from one another at their continental slopes involves about 1000 km over a 63 million year period, or an average spreading half-rate of about 0.8 cm year^{-1}. I estimate a larger minimum transform distance in order for the southern tip of Spitsbergen to clear Greenland than did Lowell: say, 550 km. A 1.6 cm year^{-1} average rate of separation caused by the creation of new crust in the Greenland and Norwegian seas thus would have required at least 34 million years since final contact to produce the present configuration. Any variations in spreading rate might increase or decrease such an estimate substantially.

If indeed rocks as young as Miocene were present in the Spitsbergen Tertiary sequence, Lowell's argument concerning the maximum possible date of folding would receive some slight support; however, the Miocene date harks back to a determination by Heer more than a hundred years ago, made on the basis of long superseded but unfortunately still quoted paleobotanical correlation (Ravn, 1922; Manum, 1962). Present concepts of the age of the entire Tertiary succession have been reviewed thoroughly by Birkenmajer (1972), who concludes as did Ravn and Manum before him that the youngest Tertiary sediments are not younger than about the beginning of the Eocene. Most of the deposits appear to be Danian and Montian, possibly passing upward into Landenian. Compression of Spitsbergen could thus have ceased at any time after about the Landenian insofar as one can tell from biostratigraphic evidence presently known from Spitsbergen.

Pitman & Talwani (1972: fig. 8), on the basis of a reconstruction of plate motions in the Atlantic area made by matching symmetrical isochronous magnetic anomalies and then computing synthetic fracture zones or flow lines, arrived at the conclusion that Spitsbergen and Greenland completed their passage past one another about 47 million years ago. Their evidence is accepted here, although the magnetic time scale on which that date is based may not correspond exactly to the radiometric scale of continental sequences bearing fossil land mammals.

The early Tertiary flora and fauna of Svalbard are well enough known to suggest a cool-temperate climate, in which *Sequoia, Ginkgo, Cercidophyllum,* and *Ulmus* are represented in addition to numerous conifers including abundant *Metasequoia.* Palms are absent, as well as various warm climate genera such as *Magnolia,* claimed by Heer to be present. Fresh-water mollusca have been

described, as has an amioid fish (Ravn, 1922; Lehman, 1951), but as yet no fossil mammals have been found (Lehmann, 1973).

SOUTHERN ROUTE

Although the De Geer Route is predicted by plate tectonic reconstructions of juxtaposed early Tertiary coasts, a second early Tertiary route across the widening Atlantic Ocean basin may have existed in the Iceland area when the Faeroe-Iceland-Greenland Ridge was created as the result of crustal swelling and simple piling up of excess tholeitic lavas emerging from a proto-Icelandic "hot spot" overlying a major site of mantle upwelling. Increasing evidence suggests that this route was subaerial, but opinions have differed concerning how much of and how long such a route remained available for terrestrial dispersal.

The southeast to northwest trending Faeroe-Iceland-Greenland Ridge is composed of igneous rocks differing in seismic velocity characteristics from both typical oceanic crust and typical continental crust. It was emplaced as Greenland separated from Rockall Bank, the Faeroes, and Norway, starting about 63 million years ago. The ridge is presently aseismic away from Iceland, but it separates areas of ocean floor with quite different spreading histories (Vogt *et al.*, 1970). The ridge is above water along approximately one third of its length at present, at Iceland, and presumably the central accreting part of the ridge has been subaerial much if not all of the time since the inception of spreading by the Icelandic plume or plumes (Burke *et al.*, 1973) at the beginning of the Tertiary. Although until a few years ago it was thought that some of the lavas on present day Iceland could be as old as 50 million years (*e.g.*, Barth, 1941: 8, translated by Dahl, 1963: 187), it has now been determined that the oldest rocks are instead only 12.5 and 16 million years old, respectively, on the southeast and northwest sides of the island (Moorbath *et al.*, 1968). Nevertheless, Iceland can be thought of as a sort of steady state phenomenon constituting a subaerial landmass of about its present size for much longer than 16 million years, any part of the land surface ultimately passing beneath the waves as spreading caused by the creation of new crust carries away that surface either northwestward or southeastward from the central accreting plate boundary that crosses Iceland. About 20 million years would appear to suffice to carry away newly created Icelandic surface to about 200 km in either direction from the plate boundary, which is in general accord with Iceland's subaerial size and with what is known about Atlantic spreading rates at that latitude. Thus the absence of rocks older than about 16 million years on present day Iceland does not mean that there was no subaerial Iceland prior to 16 million years ago; the older, sundered parts of proto-Iceland are now merely off to the sides beneath the ocean's surface and form parts of the aseismic ridge on either side of the present subaerial island.

Although Iceland's actual width as an island above sea level is of course not known or even calculated adequately for various times in the past, its present width would have filled the available width of the Atlantic Ocean about 42 million years ago [(1200–400) (63)/(1200)], assuming constant spreading rates for the sake of argument. Pitman & Talwani's (1972) results indicate greater spreading rates in

the early Tertiary, however, so that 42 million years in this simplified model is too low a figure. Error in the opposite sense is no doubt also introduced because the model does not take thermal relaxation time into account (e.g., Sclater et al., 1971).

Brooks (1973) presented evidence for an enormous Paleocene tholeitic dome overlying a mantle plume or plumes (proto-Iceland), about 200 km in observed diameter and according to him possibly as high as 6 km above sea level, occupying a position near the mouth of Kangerdlugssuaq Fjord in southeastern Greenland, against which the Faeroes would have lain. A convincing fit of Greenland with various European continental fragments has recently been prepared by Vann (1974) and this too places the Faeroes off Kangerdlugssuaq Fjord, taking into account Greenland's continental shelf. As the mantle upwelling causing the plume or plumes carried more and more material from the mantle toward the earth's surface, fissures sundered this dome, initiating plate separation. Brooks (1973: fig. 1) opts for a Y-shaped fracture, with Kangerdlugssuaq Fjord being a failed arm or aulacogen (Burke & Dewey, 1973), and it seems to me that the southern part of the Brito-Arctic Province may also play such a role. Bott et al. (1974) demonstrate that continental crust underlies the Paleocene lavas of the Faeroe Islands, which would have been continuous at that time with those of the Kangerdlugssuaq area although they are now situated some 1200 km away. Continental crust is now known to underlie Rockall Plateau as well, but that area was already separated from the British Isles by Rockall trough in the Eocene (Jones et al., 1974). It thus becomes of interest to discover, if possible, when subaerial erosion and subsidence first isolated subaerial proto-Iceland with oceanic waters as Greenland and the Faeroes retreated from the mantle upwelling under Iceland.

Nansen (1904: 74–75, 173–175) seems to have been the first to give topographic evidence of subaerial erosion of the crest of the Faeroe-Iceland-Greenland Ridge, although he explained it by postulating a much lower general sea level in the late Cenozoic. Bott et al. (1971), Fleischer (1971), and Vogt (1972a) have recently presented detailed geophysical evidence that the part of the ridge that lies between Iceland and the Faeroes was generated by the Icelandic plume or plumes during the Tertiary and stood approximately 2 km higher in the early Tertiary than at present. The deepest parts of its crest are somewhat more than 400 m beneath sea level today. This would have placed the crest well above sea level at the time of its formation, subsequent subsidence having taken place as the result of cooling, following a relaxation curve somewhat like that developed by Sclater et al. (1971) although more complex in that Sclater et al. were dealing with "normal" oceanic crust uncomplicated by the presence of an aseismic ridge. Vogt (1972b) has even suggested that the width of the ridge at any particular place is a function of the rate of magma production by the underlying plume and he therefore concluded that a slowing of ocean floor spreading occurred in the mid-Tertiary because of saddles on either side of Iceland. This would be in accord with the most recent work on magnetic anomalies near the region (Vogt & Avery, 1974). The generally flat top of the ridge from Iceland to the Faeroes, coupled with V-shaped sediment-filled valleys, suggests subaerial erosion followed by

sinking and valley filling as the spreading site over the Icelandic plume pushed the Faeroes away. West of Iceland in Denmark Strait and also at the deepest part of the Faeroe-Shetland Channel (Lightning Channel) identical depths of 583 m mark the lowest points on the crest of the Faeroe-Iceland-Greenland ridge (Huddleston, 1899: 145).

Strauch (1970) believed the final submergence of the Faeroe-Iceland-Greenland Ridge (Thulean Bridge) to have been Plio-Pleistocene in age, mainly on the basis of biological reasoning which I cannot follow. Vogt (1972a) believed that the ridge was initially breached perhaps as early as the late Eocene, about 40 million years ago, forming a shallow sill thereafter until about 30 or even 20 million years ago as calculated mainly from the paleomagnetic time scale, after which the depths increased to their present values. Vogt emphasized the effects of Miocene to present-day rapid bottom currents on the eastern flanks of the Reykjanes Ridge and Blake-Bahama Outer Ridge, but I suspect that he under-played the evidence of similar currents from 45 to 35 million years ago along the east side of the Reykjanes Ridge. Dietz & Holden (1970), Gartner (1970), Calvert (1971), Berggren & Hollister (1971), Berggren & Phillips (1971), Herman (1972), and Weaver & Wise (1974) developed the thesis that the widespread cristobalite-rich, seismically reflective, early to medial Eocene layer known as Horizon A in the North Atlantic and Caribbean is actually the geochemical result of abundant cold Arctic Ocean water reaching the Atlantic via the widening Greenland-Norwegian seas, which would have lowered the carbonate dissolution level. Such water must have crossed the crest of a submerged section of the Faeroe-Iceland-Greenland ridge if the thesis is correct. Although a substantial part of the ridge must have been above sea level, probably a greater prcentage than today because not so much ocean floor had been created, nevertheless breaks in subaerial continuity must have been sufficient by 49 million years ago both to break apart the Euramerican biota in that area and also to encourage the formation of Horizon A. Gibson & Towe (1971) have claimed, however, that a substantial influx of volcanic ash occurred in the Atlantic and Caribbean at about the same time; perhaps both causes acted in concert to produce Horizon A.

The present flora of Iceland has about twelve times as many European as American species (Dahl, 1963: 179). The flora shows subarctic rather than temperate affinities, so Dahl concluded that it cannot be merely a relict of a mid-Tertiary temperate flora but must have dispersed from western Europe to Iceland via a land continuity at least as late as the Pliocene. Dahl would thus break the Thulean Bridge first between Iceland and Greenland, then later to the east of Greenland. The Icelandic fauna shows a similar European flavor (Lindroth, 1957, 1960, 1963). Students most familiar with the Icelandic flora and fauna (see Löve & Löve, 1963, for summaries) seem generally agreed that human agencies have contributed only a minor share to these European similarities. Judged from the geology, however, it would appear that the Faeroe-Iceland-Greenland Ridge had substantial breaks in its subaerial continuity well back in the Tertiary.

Another break in continuity occurs between Greenland and Baffin Island.

Baffin Bay is the former north end of the Atlantic, opening having begun in the Mesozoic. At least in central Baffin Bay, the crust beneath a thick pile of Cretaceous and Cenozoic marine sediments (Martin, 1971) is oceanic (Barrett *et al.*, 1971). Additional rifting is indicated in the early Tertiary by volcanics on either side of the Davis Strait area, dated at about 58 million years (Keen *et al.*, 1972; Clark & Upton, 1971; Vogt, 1971), but no appreciable Cenozoic spreading of the sea floor has occurred in Baffin Bay and no Cenozoic spreading ridge or associated magnetic anomalies have been reported there (Keen *et al.*, 1971). Baffin Bay has been a formidable barrier to land organism dispersal since Mesozoic times; thus, dry-land late Mesozoic and early Cenozoic continuity of Euramerica must have lain north of Baffin Bay if such continuity existed. The effectiveness of Davis Straits as a barrier to the spread of terrestrial faunas has been discussed by Lindroth (1957, 1960, 1963) and its botanical effects have been discussed by many authors. Thus, to the extent caused by latitudinal effects whatever they may have been, the stringency of filtering on dispersal would have been about the same as would have occurred had the entire route been at the paleolatitude of northern Greenland.

Mammalian Fossil Evidence

In Table 1 I have attempted to tabulate in rather dogmatic fashion the fossil mammalian faunas of Europe at two different times in the Eocene, interpreted here to have been before and after the final break of the Euramerican biota about 50 million years ago. Endless and fruitless argument could be engaged in over issues such as the question of how much morphologic distance is appropriate for a genus, etc., but I shall simply cut that Gordian knot by listing what seems correct to me at present. Further revisions of Eocene faunas can be expected to modify details, but the main conclusion to be reached from the information given in Table 1 seems secure. I do not list other Tertiary continental faunas because there is no need to; after the medial Eocene, faunal resemblance remained at a low ebb from one side of the Atlantic barrier to the other until the Turgai Straits marine barrier within Asia was broken down at the close of the Eocene. Terrestrial faunal resemblances of western Europe with North America after that time are best interpreted as resulting from dispersal via Asia and Beringia except for a few obvious possibilities such as Arctic foxes and polar bears. For these latter animals we simply do not know the route, although the Bering Route seems most probable.

Eastern Asia's mammal fauna possessed a large endemic element from the Cretaceous to the Oligocene, but this gradually diminished in relative importance as Asian forms dispersed to North America and vice versa. Until the medial Eocene, dry-land dispersal in either direction between Asia and Europe did not occur directly, but took place rather by way of the north end of North America, where dispersal was doubly filtered, once at Beringia and again at northern Greenland. From the beginning of medial Eocene until the beginning of Oligocene time it would appear that Europe was isolated both from Asia and from North America.

Table 1. Fossil mammalian faunas of Europe at two different Eocene times.

Sparnacian 54–51 m.y. (France)	Lutetian 49–45 m.y. (France, Germany, Spain)	Overall Distribution A[a]	B[b]	C[c]	D[d]	E[e]
MULTITUBERCULATA						
Parectypodus			X			
Ectypodus			X			
MARSUPIALIA						
Peratherium			X			
	Peratherium			X		
INSECTIVORA						
cf. *Hyracolestes*		X			X	
Didelphodus			X			
Leptacodon			X			
"*Androsorex*"					X	X
"*Dormaalius*"					X	X
Adapisoriculus						X
Palaeosinopa?			X		X	
	Palaeosinopa?			X	X	
geolabidine, indet.			X		X	
amphilemurine, indet.					X	X
	Amphilemur					X
erinaceoid, indet.					X	
mixodectid, indet.					X	
Eochiromys						X
Heterohyus?					X	X
	Heterohyus					X
	Messelina					X
	Leptictidium					X
	Macrocranion					X
	Alsaticopithecus					X
DERMOPTERA?						
Placentidens						X
CHIROPTERA						
Palaeochiropteryx	*Palaeochiropteryx*					X
Archaeonycteris	*Archaeonycteris*					X
	Cecilionycteris					X
	Pseudorhinolophus					X
PRIMATES						
Plesiadapis			X			
Platychoerops						X
plesiadapid, indet.					X	
Navajovius (? = *Berruvius*)			X			
prosimian, indet.					X	
Phenacolemur			X			
Teilhardina			X			
Pelycodus			X			

[a] A, European genus also known from eastern Asia.
[b] B, European genus also known from North America.
[c] C, European genus also known from North America but taxonomic identity could be inherited from previous dispersal.
[d] D, Identification uncertain.
[e] E, Indigenous European genus at the time indicated.

TABLE 1. (continued.)

Sparnacian 54–51 m.y. (France)	Lutetian 49–45 m.y. (France, Germany, Spain)	Overall Distribution				
		A[a]	B[b]	C[c]	D[d]	E[e]
Protoadapis	Protoadapis					X
	Caenopithecus					X
	Periconodon					X
	Nannopithex					X
	Arisella?					X
	Pseudoloris					X
	Agerina					X
	Adapis					X
RODENTIA						
Paramys			X			
	Paramys			X		
Pseudoparamys						X
Microparamys			X			
Reithroparamys			X			
	Aeluravus					X
	Masillamys					X
	Gliravus					X
	Plesiarctomys					X
	theridomyid, indet.				X	X
CREODONTA						
Oxyaena			X			
Palaeonictis			X			
Tritemnodon			X			
Prototomus			X			
	"Sinopa"			X	X	
Proviverra			X			
	Proviverra			X		
Prodissopsalis	Prodissopsalis					X
cf. Prolimnocyon			X		X	
	Cynohyaenodon					X
	Creodonta, indet.				X	
CARNIVORA						
Miacis			X			
	Miacis?			X	X	
Vulpavus?			X		X	
cf. Viverravus					X	
Didymictis			X			
miacid, indet.					X	
cf. Uintacyon			X		X	
	Cynodictis					X
CONDYLARTHRA						
arctocyonid, indet.					X	
Landenodon						X
Dissacus		?X	X		X	
	Dissacus			X		
Pachyaena		X	X			
Paschatherium						X
hyopsodontid, indet.					X	
Hyopsodus			X			

TABLE 1. (continued.)

Sparnacian 54–51 m.y. (France)	Lutetian 49–45 m.y. (France, Germany, Spain)	Overall Distribution				
		A[a]	B[b]	C[c]	D[d]	E[e]
Microhyus						X
Phenacodus			X			
	Phenacodus			X		
	Almogaver					X
	Paroxyclaenus?				X	X
	Kopidodon					X
	Pugiodens					X
PANTODONTA						
Coryphodon		X	X			
TILLODONTIA						
Esthonyx			X			
PERISSODACTYLA						
Hyracotherium			X			
	Propalaeotherium	?X			X	
Lophiaspis	Lophiaspis					X
Hyrachyus?			X		X	
	Hyrachyus			X		
	Atalonodon					X
	Pachynolophus					X
	Chasmotherium					X
	Lophiodon					X
	Paraplagiolophus					X
	Anchilophus					X
	Palaeotherium					X
	Lophiotherium					X
	palaeotheriid, indet.				X	X
	lophiodontid, indet.				X	X
ARTIODACTYLA						
Protodichobune			X			
	Protodichobune					X
	Dichobune					X
	Hyperdichobune					X
	Meniscodon					X
	Catodontherium					X
	Choeromorus					X
	Dacrytherium					X
	Tapirulus					X
	Haplobunodon					X
	Mixtotherium					X
	Pseudamphimeryx					X
	Cebochoerus					X
	Rhagatherium					X

Of the 60 Sparnacian mammal genera known from Europe, 34 genera also occurred in North America but only two genera, *Pachyaena* and *Coryphodon*, are known with reasonable probability to have occurred in both Europe and Asia. Three additional genera may have occurred in both Asia and Europe, but their

identification is doubtful for one reason or another. Three of these five genera, including the certainly identified *Pachyaena* and *Coryphodon*, occur abundantly in the North American Sparnacian (Wasatchian) as well. Thus the generalized track for mammals in Sparnacian time did not run eastward from Europe but instead clearly crossed what is now the North Atlantic Ocean.

Perhaps it is appropriate to conclude this review with a quotation taken from A. R. Wallace (1881: 70). Wallace was a proponent of dispersal via land continuity if possible. His ideas contrast with what might be called the Darwinian fascination with theoretical chance dispersal: "Notwithstanding the occasional action of such [chance] causes, we cannot suppose that they have been effective in the dispersal of mammalia as a whole; and whenever we find that a considerable number of the mammals of two countries exhibit distinct marks of relationship, we may be sure that an actual land connection, or, at all events, an approach to within a very few miles of each other, has at one time existed."

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NOTE ADDED IN PROOF

While this review was in press several developments occurred which affect the geological and geophysical arguments discussed. No changes in the text have been made, but future discussants may wish to note the following:

1. Renard & Malod (1974) have presented an excellent summary of the known structure of the Barents Sea. Their references are also useful.

2. Kellogg (1975) has published important new information on the Tertiary of Svalbard that in part conflicts with arguments presented here. Kellogg believes that final separation of Greenland from Svalbard occurred by latest Oligocene or possibly early Miocene time. This seems nearly impossible to me because of the presence of very large-leaved fossil angiosperms in the youngest of the Tertiary sediments (Aspelintoppen Formation).

3. After spectacular initial success, the marine magnetic polarity time scale is in the process of being revised (Tarling, 1975). Marine magnetic anomaly 24, which is the oldest anomaly recognized between Greenland and Norway, may well be as much as 5–8 million years younger than the original estimate of 60 m.y. If true, this will affect all previous arguments based upon magnetic anomaly analysis. Anomaly 24 would then be equal in age or postdate reliable K-Ar dates on Brito-Arctic volcanics preserved on land and would be closer to the final separation date of 49 m.y. based on K-Ar control for fossil mammals.

4. During Leg 38 of the Deep Sea Drilling Project, 1974, two holes were drilled on the flanks of the Wyville Thompson Ridge. One (hole 336) reached what is identified as subaerial basaltic rubble at the edge of the flat top of the ridge northwest of the Faeroes after passing through more than 450 m of marine sediments, the base of which is dated as middle Eocene (Scientific Staff, 1975).

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